An analysis of the communication function of attack calls in little gulls

Piersma, Theunis

Published in:
Animal Behavior

DOI:
10.1016/S0003-3472(88)80160-X

Anim. Behav., 1988, **36**, 773–779

An analysis of the communication function of attack calls in little gulls

THEUNIS PIERSMA & JAN VEEN*
Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands

Abstract. The communication function of two different vocalizations, termed 'eeyit' and 'whèt', made by little gulls, *Larus minutus*, to intruders near the nest was investigated by analysing the temporal relationship between these calls and overt attack (1) under natural circumstances and (2) in two experiments with intruder dummies. Eeyit was given prior to attack, whereas whèt coincided with the attack itself. Whether or not eeyit was followed by attack depended on the reaction of the intruder to this call. Eeyit seems to carry the message 'I shall attack if provoked', whereas whèt seems to function primarily by impressing the attacked bird, and by distracting its attention during the attack. Given the existence of marked within-individual constancy of eeyit, it is argued that honest information about a bird's attack motivation is transferred by this call in all situations.

Attack behaviour is a very conspicuous part of the behavioural repertoire of nearly all bird species. For a number of larid species attack behaviour is very effective in chasing away conspecific or predatory intruders from the nesting territory (Kruuk 1964; Patterson 1965; Veen 1977). Attacks are usually preceded and accompanied by visual and/or vocal displays, which have been interpreted by earlier workers as threat signals (Tinbergen 1953, 1959; Moynihan 1955; Stout et al. 1969). Successful threatening would prevent both the sender and the receiver from engaging themselves in a potentially dangerous fight. Tinbergen (1959) suggested that the message of threat displays is effected by the transmission of honest information about the aggressive motivation of the threatening bird. Recently, the hypothesis that displays give reliable information about a bird's internal motivational state has repeatedly been criticized on evolutionary grounds, applying 'game theory' to animal contests (e.g. Maynard Smith & Price 1973; Maynard Smith 1974, 1982; Parker 1974; Caryl 1979). However, the game-theory method leads to answers that strongly depend on the kind of definitions and assumptions made (van Rhijn & Vodegel 1980; Enquist 1985). Therefore, the understanding of whether and under what conditions displays do give information about motivation and, consequently, how they function in communication, will first require more observations on animals in a variety of natural contexts (Enquist et al. 1985; Paton 1986; Paton & Caryl 1986).

In the little gull, *Larus minutus*, attack behaviour is rarely associated with visual display but always with vocalizations. In a study of agonistic interactions of little gulls (Veen & Piersma 1986) two call types, onomatopoetically termed 'eeyit' and 'whèt', were clearly associated with overt attack. Although we acknowledge that both may have communicatory significance for neighbours in the colony, partners and young, we restrict our analysis of the communication function of eeyit and whèt to the individual that is the subject of threat. Moreover, we shall consider only situations in which little gulls react to intruders into the nesting territory. The following questions were asked. (1) How are eeyit and whèt associated with attack, and what do these associations indicate about the attack motivation of the sender while calling? (2) How are eeyit and whèt reacted to by the receiver and how can its reactions determine subsequent action of the sender?

GENERAL METHODS

The observations were made on a population of little gulls in the Lauwersmeerpolder, The Netherlands (53°26′ N, 6°12′ E), described in detail by Veen (1980). In May and June 1983 two small colonies (A and B) on the 35-ha island Schoenerbult were selected for detailed study. The two colonies are described in detail by Veen & Piersma (1986). Birds incubating eggs and brooding 1–4-

* Present address: Research Institute for Nature Management, P.O. Box 9201, 6800 HB Arnhem, The Netherlands.

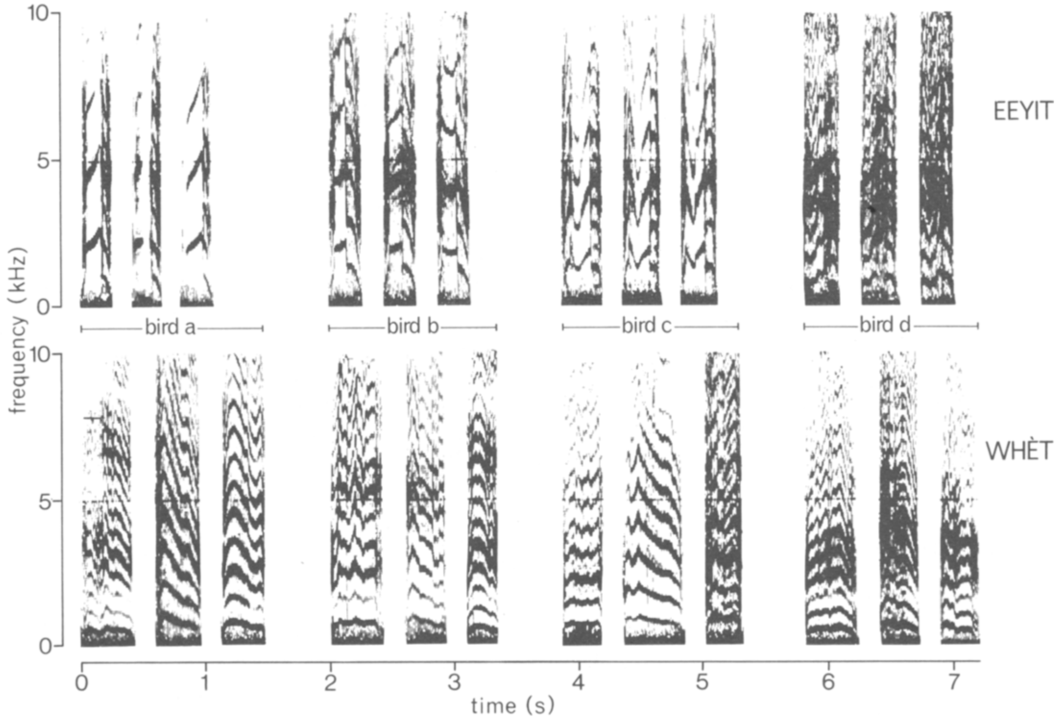

Figure 1. Examples of sonagrams of eeyit and whèt notes of different individuals in colony A. For each call type and for each individual three notes taken from different calls are presented.

day-old chicks were observed. No differences were found in the vocal and agonistic behaviour of individuals whether they were incubating eggs or taking care of chicks (see Fig. 6 in Veen & Piersma 1986).

All observations were made from blinds placed on platforms 1·2 m above ground level, at distances of 20–50 m from the nests. To distinguish individuals, some birds were marked with picric acid or rhodamine B, applied by remotely controlled dropping bottles, mounted on a stick near the nest.

Vocalizations were recorded on a Uher 4200 tape-recorder and a Sony TC D5M cassette recorder, using Sennheiser omnidirectional (MKH 105) microphones placed in the field. Vocalizations were analysed by means of a Uniscan I (type 4500) spectrum analyser (range: 0–10 000 Hz) which displays frequency/time and time/amplitude sound spectrograms on a monitor, where frequency, time and amplitude can be measured to the nearest 160 Hz, 0·018 s and 1 dB respectively. Frequency/time hard copy spectrograms were produced by photographing the display on the monitor.

During two field experiments, the visual and vocal behaviour of the little gulls were recorded simultaneously on a portable JVC videorecorder (HR 220) with a Philips camera (VK 4000, lens 75 mm).

EEYIT AND WHÈT CALLS

The physical structure of a signal may help in interpreting its possible cause and function (Morton 1977; Zahavi 1982). Figure 1 shows frequency/time spectrograms for eeyit and whèt. Both call-types are composed of a varying number of notes (from one to more than 20) of relatively long duration (eeyit: $\bar{X} \pm \text{SD} = 0{\cdot}274 \pm 0{\cdot}037$ s; whèt: $\bar{X} \pm \text{SD} = 0{\cdot}328 \pm 0{\cdot}093$ s). Eeyit notes are characterized by a three-step omega-like change in frequency, whereas whèt shows a saw-tooth-shaped frequency modulation. In addition, both show high amplitudes over a large frequency range. These characteristics make eeyit and whèt penetrate a long way and make the sender easily located (Marler 1955, 1959).

A comparison of calls of different individuals (Fig. 1) shows that for eeyit the variation is far greater between than within individuals. As regards whèt, no such individual constancy is apparent on sonagram. Although inter-individual variation is a prerequisite for individual recognition, it gives no proof that individual recognition actually occurs (Falls 1982). However, in many studies of bird vocalizations differences observable to humans when comparing sonagrams appeared to be perceptible to the birds as well (Beer 1970; Falls 1982; Veen 1985), this species included (Veen 1986). Therefore, we think that the marked individual variation of eeyit must enable individual recognition between little gulls.

Occurrence in Response to Natural Intruders

Under natural circumstances eeyit and whèt calls were most commonly recorded in the following situations: (1) in the pair-formation period, when aerial displays ended in chases and attacks on conspecifics in the air; (2) during attacks on conspecifics displaying on communal grounds; (3) during attacks on conspecific or heterospecific intruders flying over or landing near a little gull's nest; and (4) during human disturbance, by little gulls circling above or diving at the intruder. The general impression was that eeyit and/or whèt are an inseparable part of all encounters between little gulls during which attack behaviour is shown. In all cases eeyit and whèt appeared to be given by the individual performing the attack, rather than by the bird that was the subject of aggression. Whèt appeared to be more closely related to the actual attack than eeyit, and was prominently present during intense fights or prolonged attacks on persistent intruders. Eeyit calls were not always associated with physical attack. Table I shows that nesting little gulls, after being approached by natural intruders and after calling eeyit, flew up and attacked in only 30% of all cases. Moreover, flying up only occasionally resulted in physical contact; usually the intruders immediately fled. This suggests that the occurrence of attack after eeyit might depend on the reaction of the receiver to this signal.

Reactions to eeyit were studied on several occasions. Both conspecific and heterospecific intruders usually reacted with avoidance behaviour (they immediately walked or flew away from the calling bird), but eeyit calls were sometimes apparently ignored when the intruder continued approaching.

Table I. The percentage of cases in which little gulls on the nest react with eeyit to approaching intruders and subsequently attack

Intruder species	Number of observations	% Attack
Conspecifics		
Little gull *Larus minutus*	3	100%
Non-predatory intruders		
Redshank *Tringa totanus*	1	0%
Ruff *Philomachus pugnax*	4	0%
Oystercatcher *Haematopus ostralegus*	3	0%
Shelduck *Tadorna tadorna*	1	0%
Common tern *Sterna hirundo*	4	25%
Predators		
Black-headed gull *Larus ridibundus*	10	10%
Herring gull *Larus argentatus*	25	36%
Great black-backed gull *Larus marinus*	2	0%
Grey heron *Ardea cinerea*	2	0%
Marsh harrier *Circus aeruginosus*	9	55%
Total	64	30%

The data were collected during continuous watches of 5–8 h at three nests in colony A on 9 days between 28 May and 19 June.

Since under natural circumstances it was impossible to record the contextual details of the agonistic situation, which may determine the course of the interaction, we decided to do experiments in which part of the situation could be controlled.

EXPERIMENT 1

Responses to a Static Intruder Model

Methods

To study the relation of eeyit and whèt to attack once the little gulls had left their nests, an experiment was carried out in colony B on 21 June. It consisted of two 15-min tests during which a stuffed adult little gull model was placed 1 m from a breeding bird's nest. After the model had been positioned, we walked to the blind 50 m from the nest. To avoid including reactions of the breeding birds to the presence of the observers in the colony,

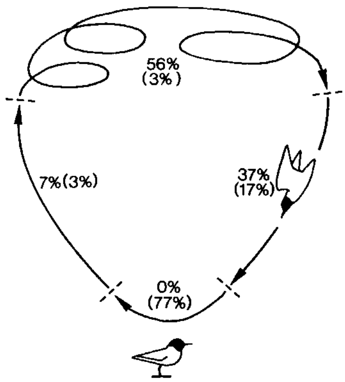

Figure 2. Percentage occurrence of eeyit notes ($N=75$) and, in parentheses, whèt notes ($N=71$) in different phases of the flight path of little gulls reacting to a stationary intruder model (stuffed little gull) placed near the nest.

observations were started 2 min after the observer had entered the hide. In both tests, one or more breeding birds nearest to the model remained circling above the model and attacked it with downward swooping flights. The visual and vocal behaviour of these individuals were recorded on video. Only observations of reactions of single birds were analysed. In the analysis of the videotape all recorded vocalizations were attributed to one of four phases of the attack flight: (1) circling above the model, (2) diving at the model, (3) attacking the model at the lowest point of the swoop, and (4) moving upwards and away from the model.

Results

Figure 2 shows that eeyit mostly occurred when the birds circled and during the downward approach of the model. A further investigation showed that the majority of eeyit calls by birds circling above the model occurred immediately before the transition to the downward swoop. As a consequence, eeyit can be regarded as associated with the moment of starting a diving attack. Whèt, however, almost exclusively occurred at the lowest point of the attack, i.e. when physical contact can be made.

These results let us conclude that eeyit and whèt, in the 'intruder at the nest' situation, are related to attack in different ways. However, the temporal relationship to attack is strong for both calls. Therefore, both can be regarded as indicating a high attack motivation.

EXPERIMENT 2

Responses to Movable Intruder Models

Under natural circumstances intruders, as a rule, are not stationary. To investigate the influence of intruder distance upon the occurrence of eeyit and whèt, a second experiment, with a movable model, was performed.

Methods

The experiment was performed in colony A in the period 7–18 June. From inside a blind, using ropes and pulleys, an intruder model (a stuffed juvenile little gull) was pulled from under a cover at 15 m distance in a straight line towards a nest. As soon as the incubating gull flew up from its nest, the model was pulled back. For all distance-intervals of 1 m between intruder and nest, the frequencies for eeyit, whèt and attack were determined. Altogether 42 tests were done at five nests. Tests during which more than one bird reacted to the model were excluded from the analysis. Details of the experimental set-up and procedure can be found in Veen & Piersma (1986).

Results

When the intruder model started its approach, the nesting birds usually changed from a resting to an alert sitting posture. We were not able to detect any change in this posture when the birds started calling eeyit and/or whèt, about half a minute later.

Both eeyit and whèt were first uttered by the nesting birds just before flying up (Fig. 3). After flying up the frequency of both calls initially increased while the birds attacked. Thereupon, with increasing distance between model and nest, both calls gradually decreased in frequency. The frequencies of eeyit, whèt and attack in relation to distance from the nest varied in parallel, i.e. they were correlated. A comparison between individuals showed the same correlation: individuals not giving eeyit or whèt in a particular test did not attack, whereas individuals giving many eeyit or whèt calls did attack frequently (Veen & Piersma 1986).

As we have shown in the earlier paper, the relationships between call and attack rate on the one hand, and the distance between the model and the nest on the other, did not change in the course of the nesting season.

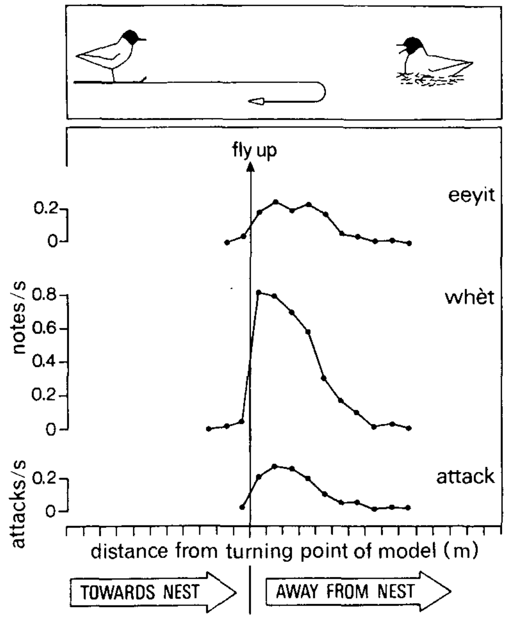

Figure 3. The average number of eeyit notes, whèt notes and attacks per unit time (s) and distance (m) when the movable little gull model was towed towards and away from the nests. Schematic representation of experimental set-up on top of figure.

EXPERIMENT 3

Reliability of Eeyit Calls

In contrast to whèt, which typically accompanies the moment of attack, calling eeyit does not necessarily lead to actual attack under natural circumstances (see above, Table I). The receiver's variable response after the sender's eeyit makes it difficult to examine whether eeyit can be considered a reliable indicator of a sender's attack motivation. For this reason we performed a modified version of experiment 2.

Methods

In this case the model was either retrieved or pulled further towards the nest by the experimenter after the first eeyit call had been given by the threatened bird on the nest. For the rest exactly the same set-up as previously described was used. In addition to a movable juvenile little gull model, a stuffed adult black-headed gull, *Larus ridibundus*, was towed towards the nesting gulls.

Eeyit is considered to be a reliable indicator of a sender's attack motivation if (1) it is followed by attack when the intruder model does not react with retreat, but instead comes nearer to the nest, and (2) it does not lead to attack from the side of the nesting bird when immediately followed by retreat of the intruder.

Table II. Attack responses of nesting little gulls to intruder models that either continued approaching or were retrieved after the first eeyit call was given by the bird on the nest

	% Attack	
Movement of model after first eeyit	Little gull model*	Black-headed gull model†
Continued approach	100% ($N=14$)	100% ($N=23$)
Retrieved	0% ($N=8$)	0% ($N=24$)

* Fisher exact test, $P=0{\cdot}00013$.
† $\chi^2_1=47$, $P<0{\cdot}001$.

Results

The results of the experiment, presented in Table II, proved to be clearcut: when eeyit was not followed by retreat of the intruder, the nesting bird invariably attacked the intruder (total number of eeyit notes before attack was on average 1·9 for the little gull model (SE = 1·3) and 7·4 (SE = 6·2) for the black-headed gull model). However, when the model was retrieved when the nesting bird started calling eeyit, the artificial intruder was never attacked. We therefore conclude that eeyit is a perfectly reliable indicator of a sender's attack motivation in the context examined.

DISCUSSION

Vocalizations associated with attack may fulfil at least two different functions. (1) They may be an integral part of the attack itself and thus help to impress the attacked bird, to distract its attention and to influence its vocal perception negatively as a result of overstimulation of its sense organs with high amplitude sounds (attack function). (2) They may signal information about the likelihood of the sender's subsequent attack (warning function). Because of their different temporal relationship to attack, whèt and eeyit are candidates for functions (1) and (2), respectively. As far as eeyit is concerned, a warning function is strongly suggested by the reactions of intruders under natural circumstances. Our results support the view that eeyit conveys the message 'I shall attack if provoked'. Since whèt is so closely related to the moment of attack, reactions to it and to attack cannot be separated. However, as can be judged from Fig. 3, whèt calls occasionally occur prior to attack. In such cases reactions to whèt were indistinguishable from those to eeyit, which suggests that whèt might serve both attack and warning functions. The occurrence of intermediate forms between eeyit and whèt in a number of calls by two individual gulls further suggests that the function of both call-types overlaps.

Paton (1986) showed that in looking at the effects of displays, it is important to separate those of posture and vocalization from those of behaviour accompanying it (e.g. locomotion) and the context in which it is given (e.g. territorial status, distance, orientation). In the case of little gulls calling eeyit when sitting on the nest, the vocalization was not accompanied by any noticeable change in posture or orientation or distance to the intruder. For this reason we are convinced that in our situation it is the call that is the relevant, and apparently reliable 'warning' signal.

The number of eeyit calls preceding attack was far greater in reaction to the black-headed gull model than to the little gull model. This suggests that the attack-warning is adapted in a quantitative way to the strength of the threat exerted by the intruder: black-headed gulls are predators on little gull chicks whereas conspecifics are rivals only.

Applying game theory, van Rhijn & Vodegel (1980) showed that individual recognition may act as a condition for honest information about the attack motivation. Among birds individual recognition on vocal cues is a common phenomenon (Falls 1982). However, this is usually effected by contact calls enabling cooperation by mates when establishing a territory, during incubation and raising of the young. In the little gull this function seems to be fulfilled by part of the Long Call (Veen 1985). The existence of individual cues in the eeyit call, in addition to the Long Call, is a striking feature regarding the function of this call. It suggests selection pressure on individual recognition of a threatening bird by its opponent. If this is indeed the case, honest information about the attack motivation could be the consequence, irrespective of the type of contest (asymmetric, as in the experimental situation, or symmetric) in which eeyit is given.

ACKNOWLEDGMENTS

We are most grateful to G. P. Baerends and J. G. van Rhijn for their constructive criticism and stimulation throughout the preparation of this paper and to J. Hogan, B. Ens, H. Prins and two anonymous referees who also commented on earlier drafts. L. Hoekstra and J. Nijboer prepared the dummy models, H. Lochorn-Hulsebos typed the manuscript and D. Visser helped with the figures. We also thank the 'Rijksdienst voor de IJsselmeerpolders' for permission to work in the nature reserve under their management.

REFERENCES

Beer, C. G. 1970. Individual recognition of voice in the social behaviour of birds. *Adv. Study Behav.*, **3**, 27–74.

Caryl, P. G. 1979. Communication by agonistic displays: what can games theory contribute to ethology? *Behaviour*, **68**, 136–169.

Enquist, M. 1985. Communication during aggressive interactions with particular reference to variations in choice of behaviour. *Anim. Behav.*, **33**, 1152–1161.

Enquist, M., Plane, E. & Roëd, J. 1985. Aggressive communication in fulmars (*Fulmarus glacialis*) competing for food. *Anim. Behav.*, **33**, 1007–1020.

Falls, J. B. 1982. Individual recognition by sounds in birds. In: *Acoustic Communication in Birds. Vol. 2* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 237–278. New York: Academic Press.

Kruuk, H. 1964. Predators and anti-predator behaviour in the black-headed gull (*Larus ridibundus*). *Behav. Suppl.*, **11**, 1–130.

Marler, P. 1955. Characteristics of some animal calls. *Nature, Lond.*, **176**, 6–7.

Marler, P. 1959. Developments in the study of animal communication. In: *Darwin's Biological Work* (Ed. by P. R. Bell), pp. 150–206. London: Cambridge University Press.

Maynard Smith, J. 1974. The theory of games and the evolution of animal conflicts. *J. theor. Biol.*, **47**, 209–221.

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.

Maynard Smith, J. & Price, G. A. 1973. The logic of animal conflicts. *Nature, Lond.*, **246**, 15–18.

Morton, E. S. 1977. On the occurrence and significance of motivation–structural rules in some bird and mammal sounds. *Am. Nat.*, **109**, 17–34.

Moynihan, M. 1955. Some aspects of reproductive behaviour in the black-headed gull (*Larus r. ridibundus L.*) and related species. *Behav. Suppl.*, **4**, 1–201.

Parker, G. A. 1974. Assessment strategy and the evolution of fighting behaviour. *J. theor. Biol.*, **47**, 223–243.

Paton, D. 1986. Communication by agonistic displays: II. Perceived information and the definition of agonistic displays. *Behaviour*, **99**, 157–175.

Paton, D. & Caryl, P. G. 1986. Communication by agonistic displays: I. Variation in information content between samples. *Behaviour*, **98**, 213–239.

Patterson, I. J. 1965. Timing and spacing of broods in the black-headed gull. *Ibis*, **107**, 433–453.

van Rhijn, J. G. & Vodegel, R. 1980. Being honest about one's intentions, an evolutionary stable strategy for animal conflicts. *J. theor. Biol.*, **85**, 623–641.

Stout, J. F., Wilcox, J. R. & Creitz, L. E. 1969. Aggressive communication by *Larus glaucescens*. Part I. Sound communication. *Behaviour*, **34**, 29–41.

Tinbergen, N. 1953. *The Herring Gull's World.* Collins: London.

Tinbergen, N. 1959. Comparative studies of the behaviour of gulls (Laridae): a progress report. *Behaviour*, **15**, 1–70.

Veen, J. 1977. Functional and causal aspects of nest distribution in colonies of the sandwich tern (*Sterna s. sandvicensis* Lath.). *Behav. Suppl.*, **20**, 1–193.

Veen, J. 1980. Breeding behaviour and breeding success of a colony of little gulls *Larus minutus* in the Netherlands. *Limosa*, **53**, 73–83.

Veen, J. 1985. On the functional significance of Long Call components in the little gull. *Neth. J. Zool.*, **35**, 63–86.

Veen, J. 1986. The crested tern and the supermarket. *Anim. Behav.*, **34**, 937–939.

Veen, J. & Piersma, T. 1986. Causation and function of different vocal reactions of little gulls *Larus minutus* to intruders near the nest. *Behaviour*, **96**, 241–264.

Zahavi, A. 1982. The pattern of vocal signals and the information they convey. *Behaviour*, **80**, 1–8.

(Received 10 April 1987; revised 6 August 1987; MS. number: 3002)